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A LIMNOLOGICAL INVESTIGATION OF PERIPHYTON IN DOUGLAS LAKE, MICHIGAN[1]

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This paper is based upon results of a limnological investigation of periphyton in Douglas Lake, Michigan, an unmodified, fresh-water, temperate lake of the second order. Stress has been placed upon a survey of organisms involved, environmental factors most influential in periphyton development, and upon the limnological role of this material. By periphyton is meant that assemblage of organisms growing upon free surfaces of submerged objects in water, and covering them with a slimy coat. It is that slippery brown or green layer usually found adhering to the surface of water plants, wood, stones, or certain other objects immersed in water and may gradually develop from a few tiny gelatinous plants to culminate in a woolly, felted coat that may be slippery, or crusty with contained marl or sand.

Because of its constant occurrence particularly in summer, sizeable quantities produced, its seasonal successions, and other phenomena, periphyton seems to play an important role in limnological processes of a lake and merits careful investigation. Periphyton appears to have been almost entirely neglected in America, and in Europe has received scant attention in comparison to other aspects of fresh-water life.

Seligo (1905) called periphyton *Aufwuchs*, a term adopted by many investigators. Hentschel (1915) used *Bewuchs* in a slightly wider sense, but Willer (1920) used *Aufwuchs* to describe growths occurring on living substrata, and *Bewuchs*, that on dead supports. Lenz (1928) and Naumann (1931) accepted this usage. Behning (1924) introduced the word *periphyton* to designate only material growing on artificial objects in water. Roll (1939) proposed that *periphyton* be used with the meaning indicated in the first

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paragraph of the present work. This term is preferable, but it should be understood that it does not include those organisms considered as belonging to benthos.

Studies, such as those of Kurz (1912) and Torka (1935), simply listed plants found in periphyton. However, Hentschel (1915, 1917) made limnological studies of periphyton on glass slides, in aquaria, and on floating marine plants. In a similar fashion, Wesenberg-Lund (1908) studied algae on beach stones, Willer (1920, 1923) organisms on living substrata, and Naumann (1925) colonial algae on various substrata. Periphyton of littoral situations was studied by Borner (1921), and Brehm and Ruttner (1926).

Investigations of a practical nature were made by Naumann (1929, 1933, 1934a, and 1934b) to aid waterworks engineers, and by Hentschel (1925) for detection of pollution. Behning (1928) studied periphyton in relation to the Volga fisheries. Hentschel (1923) and Visscher (1928) studied fouling of ships' bottoms.

Little study has been made on periphyton on the bulrush (*Scirpus validus* Vahl), which grows on Big Shoal in Douglas Lake. Surface of the bulrush facilitates removal of periphyton and area is easily measured. Physico-chemical conditions and depth are rather uniform on Big Shoal, though wave action is, at times, strong. The reader is referred to Moffett (1943) for morphometric and dynamic features of Big Shoal.

Periphyton on twigs of brush shelters installed by Rodeheffer (1939) was studied; also that on stones which occur in localized areas near the lake's margin.

Methods

Methods used in the present investigation were modelled largely after those suggested by Thomasson (1925) and used by Meschkat (1933, 1934a, 1934b, 1934c) and Meuche (1939) for the study of periphyton on stems of plants. Collection of the bulrush on which periphyton was growing was made by grasping the emergent portion, cutting it off at the base, and removing it as gently as possible to avoid washing off the filmy covering. The recently submerged portion was then cut into sections 20 cm long, representing a stratum of that depth in the water. Thus, the first section came from the stratum of water extending from the surface to 20 cm below it; the next deeper section from the stratum 20 cm deep to 40 cm and so on. From each section was cut a sample 3–4 cm long which was preserved in four per cent formalin for later examination. In each instance samples were taken from three or four culms. The samples were then scraped to remove the periphyton, measured, and their lateral area computed. When possible, the material was examined while still alive. A similar procedure was used to get samples from brush shelters.

To count the organisms, the compact, fibrous mass of periphyton had

to be teased apart. This was best done in a long, narrow cell made of strips of glass cemented together. Its capacity of 72 cc was sufficient to hold the scraped-off sample in its preservative. Larger organisms, such as *Gloeotrichia* and chironomid larvae, were counted with a binocular dissecting microscope. Diatoms and other small organisms were counted in a Sedgwick-Rafter counting cell, using the low power of a compound microscope equipped with a Whipple ocular micrometer. All rotifers and nematodes in the whole cell were counted, but diatoms and desmids were counted in square units of one cubic millimeter each. Using the volume of the sample and the area from which each was taken, the number of organisms per square decimeter was calculated.

Samples were centrifuged for two min. at 1,000–2,000 r.p.m.; the volume of periphyton was measured by means of a graduated centrifuge tube. The sample was then filtered, and dried at a temperature of not more than 60°C. for not less than two hours, according to the technique described by Borutzky (1935). Subtracting the weight of the filter paper from the total weight gave the dry weight of the sample. Volume and weight were then expressed in terms of the amount per square decimeter of bulrush surface.

A deep, hollow square made of sheet brass was used to measure the area of stone or log from which periphyton was taken. It was sharpened on its lower edge, so that when pushed down into the encrusted material, it cut through to the substratum and enclosed a measured area. Material outside the square was then scraped away. When the square was lifted, periphyton of the measured area could then be scraped off with little error. Examinations and calculations were made in the same manner as already described except that the presence of sand made centrifuging, drying, and high magnification counting impracticable.

Samples of periphyton on bulrushes were collected at intervals along a transect lakeward, at depths of 20, 40, 60, 80, and 100 cm. These examinations were designed to discover the distribution of periphyton at different depths and the possible relationship between it and turbulence resulting from wave action.

This study was carried on during the summers of 1936 to 1941 inclusive and under the direction of Professor Paul S. Welch to whom indebtedness is here expressed.

Organisms Composing Periphyton

All organisms found in periphyton are included in the list in Table 1. It is possible that representatives of a few planktonic or benthic species entangled in the periphyton are included. Organisms are described as many (m) or few (f), contingent upon the frequency of their appearance. At times certain species were present in large numbers, but *many* is used to indicate a steady plenitude. *Scirpus* culms were classified as dead or living depending

on whether they were brown, soft, and fragile, as are those which grew the year previous to collection, or whether they were young, green, and strong.

In many cases identification was not carried to species because wide variety of forms made this impracticable, and, for the purposes of this paper, it was not necessary.

TABLE 1. Organisms found in periphyton on bulrushes, brush shelters, and stones.

Name of organism	On *Scirpus* culms		On brush shelters	On stones	Name of organism	On *Scirpus* culms		On brush shelters	On stones
	Live	Dead				Live	Dead		
Pennales					*Vorticella campanula* Ehrenberg		f	f	
Tabellaria flocculosa (Roth) Kützing	m	m	m	m	*Ophrydium sessile* Kent			f	m
Tabellaria fenestrata (Lyngbye) Kützing	m	m	m	m	Porifera				
Fragillaria capucina Desmaz	m	m	m	m	*Spongilla* sp.				f
Synedra ulna (Nitzsch) Ehrenberg	m	m	m	m	*Ephydatia* sp.			f	
Navicula sp.	m	m	m	m	Coelenterata				
Navicula sp.	m	m	m	m	*Pelmatohydra oligactis* (Pallas)	m	m	f	f
Pinnularia viridis (Nitzsch) Ehrenberg	f	m	m	f	Nematoda	f	f	f	f
Pinnularia nobilis Ehrenberg	f	m	m	f	Rotifera				
Pinnularia sp.	f	m	m	f	*Dicranophorus* sp.	f	m	m	
Gomphonema sp.	m	m	m	m	*Dicranophorus forcipatus* (Ehrenberg)	f	m	m	f
Ghomphonema sp.	m	m	m	m	*Euchlanis dilatata* Ehrenberg	f	m	m	f
Cymbella cymbiformis (Kützing) Brébisson	m	m	m	m	*Floscularia janus* (Hudson)			f	
Epithemia argus (Ehrenberg) Kützing	m	m	m	m	*Lepadella* sp.		f		
Epithemia sp.	m	m	m	m	*Monostyla lunaris* (Ehrenberg)	m	m	m	f
Chlorophyceae Tetrasporales					*Philodina* sp.		f		
Sphaerocystis sp.		f	f	f	*Ptygura mucicola* (Kellicott)	m	m		
Gloeocystis gigas (Kützing) Lagerheim	f	m	m		*Rotaria elongata* (Weber)	f	f	f	
					Rotaria rotatoria (Pallas)	f	f	f	
Ulotrichales					*Scaridium longicaudum* (Müller)	f	f		
Microspora sp.	f	f	f		*Trichotria pocillum* (Müller)	f	f		
Stigeoclonium sp.				f					
Chaetophora incrassata (Hudson) Hazen			m	m					
Protoderma sp.		f	f		Gastrotricha				
Coleochaete pulvinata Brébisson	f	f	f		*Chaetonotus* sp.		f		
Chaetosphaeridium globosum (Nordstedt) Klebahn		f			Oligochaeta				
					Aeolosoma sp.		f		
					Chaetogaster sp.	f	f	f	
Oedogoniales					*Chaetogaster* sp.	f	f		
Oedogonium sp.		f	f		*Nais* sp.				f
Bulbochaete sp.		f	m	m	*Stylaria lacustris* (Linnaeus)	f	f	f	f

TABLE 1.—Continued

Name of organism	On *Scirpus* culms		On brush shelters	On stones	Name of organism	On *Scirpus* culms		On bush shelters	On stones
	Live	Dead				Live	Dead		
Naidium osborni Walton	f	m	m	f	Heterokontae				
Pristina sp.		f			Heterococcales				
					Botryococcus sp.		f		
Ephemerida									
Baetidae nymphs				f	Bacillarieae				
					Centrales				
Trichoptera					*Melosira crenulata*				
Larvae	f	f	f		(Ehrenberg) Kützing	m	m	m	m
					Melosira granulata				
Diptera					(Ehrenberg) Ralfs	m	m	m	m
Chironomidae					*Cyclotella* sp.		f		
Chironomus sp. larvae	f	f	f	f					
Chironomus sp. larvae	f	f	f		Pennales				
Chironomus sp. larvae				f	Chlorococcales				
					Pediastrum boryanum				
Other Diptera					(Turpin) Meneghini	f	f	f	f
Corynoneura sp. larvae		f			*Dictyosphaerium* sp.		f	f	
Ceratopogoninae larvae				f	*Scenedesmus* sp.	f	f	f	
Bryozoa					Siphonales				
Plumatella sp.		f	f	f	*Vaucheria* sp.		f	f	
Myxophyceae					Zygnematales				
Chroococcales					*Mougeotia* sp.	f	f	m	
					Zygnema sp.	f	f	f	
Gloeocapsa sp.	m	m	m	m	*Cosmarium protactum*				
Chroococcus sp.	m	m	m	m	(Nägeli) DeBary	m	m	m	f
Chroococcus turgidus					*Cosmarium reniforme*				
(Kützing) Nägeli	f	m	m	m	(Ralfs) Archer	m	m	m	f
Rhabdoderma sp.		f	f	f	*Cosmarium* sp.	m	m	m	f
Gloeothece sp.		f	f	f	*Gymnozyga* sp.		f	f	
Merismopedia sp.		f	f	f					
Gomphosphaeria sp.	f	m	m		Fungi				
Aphanothece sp.	f	f	f	f	Bacteria	m	m	m	m
Aphanocapsa sp.		f	f	f	Phycomycetes	m	m	m	m
Microcystis flos-aquae									
(Wittrock) Kirchner	f	f	f		Protozoa				
					Mastigophora				
Hormogonales					*Euglena viridis*				
Spirulina sp.		f	f		Ehrenberg		f		
Oscillatoria sp.	f	f	f	f					
Lyngbya sp.	f	f	f	f	Sarcodina				
Anabaena sp.			f		*Amoeba* sp.		f		
Cylindrospermum sp.		f			*Amoeba verrucosa*				
Scytonema sp.			f	f	Ehrenberg		f		
Tolypothrix tenuis					*Amoeba proteus* Leidy		f		
Kützing			m	m	*Vahlkampfia* sp.		f		
Stigonema sp.	f	f	f		*Pyxidicula* sp.		f		
Hapalosiphon sp.		f			*Centropyxis aculeata*				
Rivularia dura Roth			f		Stein		f		
Gloeotrichia Pisum					*Difflugia pyriformis*				
(Agardh) Thuret	m	m	f		Perty		f	f	
					Pompholyxophrys sp.		f		

TABLE 1.—Continued

Name of organism	On *Scirpus* culms		On brush shelters	On stones	Name of organism	On *Scirpus* culms		On brush shelters	On stones
	Live	Dead				Live	Dead		
Ciliata					Copepoda				
Colpoda helia Stokes		f			*Cyclops* sp.	f	f	f	f
Stentor igneus Ehrenberg		f							
Aspidisca lynceus					Ostracoda				
Ehrenberg		f			*Cypridopsis vidua*				
					O. F. Müller	f	f	f	f
Cladocera									
Sida crystallina					Malacostraca				
(O. F. Müller)	f	f	f	f	*Hyalella knickerbockeri*				
Ilyocryptus sordidus					(Bate)	f	f	f	
(Liévin)	f	f	f	f					
Camptocercus rectirostris					Hydracarina				
Schoedler		f			*Arrhenurus* sp. larvae	f	f		
Pleuroxus hamulatus					Oribatidae nymphs				f
Birge	f	m	m	f					

Explanation: *m* stands for many; *f* for few; where space is left blank, no organisms of that kind were seen.

Both Table 1 and Table 2 show the diversity of the biota found in periphyton. The number of genera and species of animals found is 47 and 54, respectively; of plants, 51 and 61, respectively. Of a total of 98 genera, only 13 have more than one species and of them but five are animals. Diatoms have the largest number of species for the number of genera. Based on the count of species and of individuals diatoms were most numerous with Rotifera and Hormogonales vying for second place. Since identification of fungi was not attempted, no statement is possible here concerning the genera, but the number of individuals was very large. The prevailing groups in periphyton were the diatoms, fungi, Hormogonales, and rotifers.

TABLE 2. Number of genera and species in certain groups occurring in periphyton.

Plant groups	Genera	Species	Animal groups	Genera	Species
Myxophyceae			Sarcodina	6	8
Chroococcales	9	10	Rotifera	10	12
Hormogonales	11	11	Oligochaeta	6	7
Bacillarieae	10	17	Cladocera	4	4
Chlorophyceae	18	20	Diptera	4	6

EFFECT OF WAVES

The area on Big Shoal in which the bulrushes grew is subjected to considerable wave action (Moffett, 1943) caused by prevailing northwest winds. It provides a good place to study the effect of wave action on periphyton growing on bulrushes. Counts made at different levels on the culms as given

under "Methods" showed the greatest fluctuation in the stratum extending from the surface down to 40 cm below it where wave action is most intense. Fewer organisms occurred here than lower down, but among them the most abundant were *Gloeotrichia* which adhere very tenaciously to the bulrushes. After heavy wave action populations were considerably reduced, but recovery to the amount usually found was quicker here than in lower strata. For that reason greatest changes in numbers of organisms took place in this region, especially from the surface down to 20 cm below it. Tables showing the number of organisms at different levels are on file, but could not be included in the present paper because of lack of space.

The diatom-fungus mat covering the culms, formed by felted fibers of fungi, filamentous algae and diatoms, was heavier in the lower levels—below 40 cm beneath the surface. Oligochaetes and crustaceans were usually

TABLE 3. Average number of organisms per square decimeter found on live *Scirpus* on dates given, Big Shoal, 1937.

Name of organism	7/12	7/15	7/20	7/27	7/30	8/7	8/14	8/21
Gloeotrichia	386	760	480	70	85	130	235	230
Pelmatohydra	85	50	95	85	155	25	20	2
Oligochaeta	30	50	45	12	10	45	90	40
Crustacea	5	15	15	10	8	25	70	55
Diptera (mostly Chironomidae)	10	3	5	10	2	5	10	15
Total macroscopic animals	140	95	180	140	180	100	180	170
Centrifuged volume in cc	1.0	1.0	0.9	1.4	1.0	2.0	2.6	3.0
Dry weight in mg	15	35	20	40	30	60	55	130

TABLE 4. Average number of organisms per square decimeter found on dead *Scirpus* on dates given, Big Shoal, 1937.

Name of organism	7/14	7/24	7/27	8/2	8/9	8/16	8/21
Gloeotrichia	560	150	245	225	25	240	240
Pelmatohydra	30	110	120	35	2	1	2
Oligochaeta	75	0	35	53	50	45	65
Crustacea	35	0	20	20	60	115	20
Diptera (mostly Chironomidae)	10	0	5	10	10	10	15
Total macroscopic animals	175	120	190	130	150	185	110
Centrifuged volume in cc	1.0	1.8	3.0	3.1	2.5	3.0	2.8
Dry weight of sample in mg	180	55	45	115	55	95	130

more abundant here, preferring conditions offered by the mat. After severe wave action less fluctuation in number of organisms was observed in the 40–60 cm level than in any other stratum. *Gloeotrichia*, however, had their smallest loss in the stratum 60–80 cm deep.

The best measure of productivity was the average number of organisms found in all levels, because, as in the instance of *Gloeotrichia*, when an organism was abundant it was usually so over the whole culm. For this reason, the numbers given in Tables 3–8 are averages of the number of

organisms found at the different levels on the 3–4 culms from which samples were taken.

To discover changes in periphyton, collections were made on July 24 and 27, 1937; August 12, 1938; and July 17, 1939 just after heavy winds had lashed the lake (Tables 3–8). Decreases predominated especially on live culms to 40 or 60 cm depth. Even the adherent *Gloeotrichia* declined sharply in upper levels. Among animals, Crustacea and Chironomidae showed greatest decrease. Increases were common below the 60 cm depth, but, on living culms, were usually small. Dead culms, not pushed over by

TABLE 5. Average number of organisms per square decimeter found on live *Scirpus* on dates given, Big Shoal, 1938.

Name of organism	6/26	7/2	7/12	7/16	7/23	8/2	8/12	8/18
Gloeotrichia	20	75	180	225	570	440	530	140
Pelmatohydra	115	0	0	2	5	15	10	280
Oligochaeta	80	25	25	35	45	130	40	10
Crustacea	40	135	30	30	15	82	102	3
Diptera (mostly Chironomidae)	54	22	25	25	20	20	10	5
Total macroscopic animals	300	185	85	105	90	250	175	300
Centrifuged volume in cc	0.6	1.1	0.8	1.3	1.2	2.7	2.3	0.7
Dry weight of sample in mg	20	25	25	30	20	35	33	20

TABLE 6. Average number of organisms per square decimeter found on dead *Scirpus* on dates indicated, Big Shoal, 1938.

Name of organism	6/26	7/2	7/12	7/16	7/23	8/2	8/12	8/18
Gloeotrichia	53	227	203	100	127	283	388	517
Pelmatohydra	50	0	2	5	7	12	13	12
Oligochaeta	435	227	75	72	45	53	58	63
Crustacea	597	882	165	23	23	45	72	47
Diptera (mostly Chironomidae)	40	40	18	25	18	18	18	12
Total macroscopic animals	1140	1172	266	125	88	168	171	150
Centrifuged volume in cc	9.2	6.2	2.5	1.9	1.3	2.1	2.7	2.4
Dry weight of sample in mg	358	172	78	52	45	42	95	45

the heavy waves, usually lost less periphyton than live ones. The counts of *Gloeotrichia*, Oligochaeta, Crustacea, Chironomidae, and volume of solid matter showed practically as many instances of decrease as increase. The surface of dead culms is not slick and wax-like (as is that of live ones) so that periphyton organisms can adhere better. Thus wave action affects live-culm periphyton more than that on dead culms.

During calm periods, increases in periphyton were apparent and the reverse during windy weather, especially on live culms. *Gloeotrichia*, *Pelmatohydra*, Oligochaeta, Crustacea, and volume of solid matter increased (Tables 3–4) under the calm conditions of the early summer of 1937. Commencing with the storm already mentioned, a period of windy weather set in, during which most organisms were reduced in numbers. Hydras thrived during this period, whereas previously they had appeared to be covered by

the diatom-fungus mat. As conditions became quieter near the close of the summer, hydras practically disappeared, and other organisms increased. Thereafter, weather became more unsettled with consequent decline in populations.

Early summer of 1938 (Tables 5–6) was marked by windy conditions, the mid-season by calmer weather, and late summer by winds. *Gloeotrichia*

TABLE 7. Average number of organisms per square decimeter found on live *Scirpus* on dates given, Big Shoal, 1939.

Name of organism	6/24	7/8	7/17	7/24	7/31	8/7	8/14	8/18
Gloeotrichia	72	255	232	240	770	700	485	700
Pelmatohydra	0	2	0	16	85	155	27	9
Oligochaeta	33	78	97	53	100	70	63	63
Crustacea	28	52	20	3	34	7	64	170
Diptera (mostly Chironomidae)	8	32	10	8	2	5	12	12
Total macroscopic animals	78	165	160	78	220	190	255	260
Diatoms (in millions)	5.8	4.9	7.5	3.2	4.4	2.6	5.8	7.8
Desmids (in thousands)	97	102	91	44	49	2800	100	95
Nematoda	170	32	110	93	240	40	70	700
Rotifera	750	270	570	630	920	900	2100	3000
Centrifuged volume in cc	0.7	1.4	0.8	0.4	1.4	0.9	2.8	2.8
Dry weight of sample in mg	18	32	14	20	60	32	50	140

TABLE 8. Average number of organisms per square decimeter found on dead *Scirpus* on dates given, Big Shoal, 1939.

Name of organism	6/24	7/8	7/17	7/24	7/31	8/7	8/14	8/19
Gloeotrichia	55	110	640	250	730	470	650	410
Pelmatohydra	0	0	0	12	5	53	5	5
Oligochaeta	210	140	180	125	180	70	60	70
Crustacea	192	130	42	75	280	55	73	185
Diptera (mostly Chironomidae)	18	15	5	10	22	16	10	17
Total macroscopic animals	420	240	250	225	490	212	155	280
Diatoms (in millions)	53	8	9	9	9	13	8	9
Desmids (in thousands)	103	68	151	67	67	57	52	78
Nematoda	1400	2330	660	450	1340	540	350	1520
Rotifera	3100	950	1750	750	2380	1400	1980	2270
Centrifuged volume in cc	3.1	2.4	1.9	2.0	3.2	2.3	2.5	3.3
Dry weight of sample in mg	100	185	42	78	105	35	58	60

and volume of periphyton increased to a maximum in late July to mid-August, whereafter both declined. Hydras, as usual, diminished sharply as *Gloeotrichia* increased, then waxed at season's close when *Gloeotrichia* waned. Oligochaeta and Crustacea showed two maxima with a minimum close to mid-July. All organisms, except hydras, dwindled at summer's end.

Unsettled weather conditions of 1939 were reflected in irregular population changes. All organisms but hydras increased during the first two weeks, but received a set-back by windy weather that lasted until late July. Calm conditions fostered increase until windy weather set in early in August, during which period only hydras thrived. During the remainder of the summer little population change occurred.

In general, all organisms fluctuated together, increasing in early July and declining late in the same month. Oligochaetes, crustaceans, and dipterous larvae, during this study, usually rose and fell with *Gloeotrichia*. *Pelmatohydra* usually fluctuated in inverse fashion with *Gloeotrichia*. No variation of planarians, *Chaetogaster*, *Stylaria*, rotifers, nematodes, or chironomid larvae was evident.

Comparison of periphyton found on bulrushes in situations exposed to considerable wave action with that in protected places gave results which showed the detrimental effect of waves. More filmy periphyton of greater amount, with filamentous algae predominating, was found in protected bays whereas the mat had a firmer texture and was more closely appressed to the culm on the exposed shoals.

Near shore, where waves produce surf, turbulence is greater than in deeper water where waves are unmodified. To determine the relation between depth of water in which bulrushes stood and periphyton growing on them, transects were made from shore lakeward, samples being taken from live culms growing where water was 20, 40, 60, 80, and 100 cm deep. It was found that the number of *Gloeotrichia* was small throughout the season where water was 20 cm deep. Little of anything else was present. As the season progressed there was a slight increase in populations, especially at depths greater than 40 cm but very seldom did the numbers exceed those in clumps under observation standing out in water 1.2 m deep.

A similar transect, made in the less exposed Marl Bay where prevailing northwest winds have less chance to cause strong wave action, showed, in general, a greater number of organisms on the exposed Big Shoal. However, centrifuge volume of Marl Bay samples far exceeded that of Big Shoal, indicating that more filamentous algae grew on Marl Bay bulrushes. Greater numbers of *Gloeotrichia* and *Pelmatohydra* were found on the exposed shore at a depth of 80 cm but, at 1.0 m, the less exposed shoal showed greater numbers of all organisms.

In the upper stratum of shallow water, *Sida crystallina* were found clinging to the surface of bulrushes as long as it was clean of periphyton—which was in the early summer. They also were found on clean glass slides and clean stones. They were common in plankton as well. In late summer, after the mat had grown, *Pleuroxus* was most abundant, whereas *Sida* was present in small numbers or not at all. Again mention must be made that tables are on file from which these conclusions are drawn.

Origin of Some Plankton Drift

To find out if periphyton occurs in plankton drift, examination was made of the grayish, flocculent material that accumulated along shore following protracted on-shore wind. With the microscope small tufts containing fungal hyphae covered with diatoms could be seen in the drift.

They resembled pieces of fungus-diatom mat from bulrushes. Plankton catches, taken with a net in the bulrush clump on Big Shoal, contained similar small clusters of woolly material. It was clear that the drift must have come from the clump since other material, such as cut segments of culms and leaves from brush shelters, could have had no other source. Periphyton could have been dislodged by the washing action of waves or by bulrushes rubbing against one another.

To ascertain whether bulrush periphyton could break down into the kind of tufts found in plankton drift, some of it was subjected to shaking in a machine designed by one of the author's fellow students. Samples in vials were shaken at 206 horizontal strokes per minute. After five minutes, the fuzzy clumps had broken into smaller ones. Small clumps of fungus, broken filaments, and oil droplets were common. In another machine, designed by the same person, periphyton was churned in water by a vertically oscillating paddle. Results were the same as in the preceding experiment after 80 minutes at 200 strokes per minute. In both cases the small clumps obtained resembled closely the material in plankton drift. Evidently strong wave action dislodges periphyton from bulrushes and some plankton drift is thus formed, as some of it is undoubtedly the broken-down remains of dislodged fungus-diatom mat.

Effect of Waves on Periphyton on Stones

A transect was made from shore lakeward and samples were taken from stones at depths of 20, 40, and 60 cm to discover the effect of waves on periphyton. The number of animals per square decimeter, in general, was found to be greater at 60 cm depth than in shallower water, especially chironomids and crustaceans. Oligochaetes were present in about the same numbers at all depths. Bryozoans were found only at depths exceeding 60 cm. It appears that wave action, combined with ice action keeps the stones bare of periphyton in water 20 cm deep. Only stones about 15–30 cm in diameter were considered since smaller ones were protected by their large neighbors and were either well covered by periphyton or buried beneath sand. As much as 80–90 per cent of the upper surface of the stones in shallow water was bare, whereas only about 10 per cent was clean at 60 cm depth and none at depths of 80–100 cm. Periphyton grew to be 10–12 mm thick at these greater depths.

Periphyton and Substratum

effect of substratum on periphyton

Since periphyton is not uniformly distributed on the same culm and adjacent, similar culms are not covered with the same amount, the question arises whether difference in substratum encourages periphyton on one culm and hinders it on another. Examination of the tissues of the culm surface

discloses no apparent difference between two such living culms. However, surfaces of living and dead culms differ widely in physical features. Live ones have a waxen surface which is hydrofuge, slick, and easily cut with a knife. The dead culm has lost its smooth surface. It is soft, friable, flabby, and dark brown. Under magnification, cells were seen to be empty, whereas living tissue was abundantly fibrous, white, and translucent. Black, or dark gray threads, probably the mycelia of fungi, had penetrated the empty cells of the dead culms. Their rough, easily penetrated surface provides a better substratum to which periphyton organisms can adhere. Dead culms thus had a greater average volume and dry weight of periphyton than live ones (Tables 3–8).

To compare growth of periphyton on different living substrata, samples were taken of *Phragmites* and *Scirpus* which were growing together in the same clump on an exposed shoal, in 60 cm of water. More *Gloeotrichia*, Crustacea, and centrifuged volume of periphyton were found on *Phragmites* at or near the bottom than in upper levels. Growth on *Scirpus* was distributed chiefly in the opposite way: the greater amount was found near the surface, or farther from the bottom. Much more filamentous algae grew on *Phragmites*, accounting for the greater centrifuged volume of periphyton on these plants, as well as more *Gloeotrichia* and Crustacea. Different substrata apparently is the factor causing the disparity since habitat was the same for both.

Periphyton on non-living differs from that on living substratum. Growth on manila ropes and cotton sash cord was of a different appearance and composition from that found on *Scirpus* growing nearby, even though organisms found on the ropes were also on bulrushes. No *Gloeotrichia* grew on rope, nor on glass slides even though these hung within a clump of bulrushes. No *Flosculariа* or *Rivularia* were found on *Scirpus*. In these cases, too, substratum was the only factor which was different.

Dry wood produced a growth of periphyton in less time than green wood. In brush shelters, aspen twigs had the greatest growth of periphyton within two weeks after being put into water, oak was second, alder third, and maple had least of all. Cedar dock posts also had less than aspen. Even after a year's submergence aspen still led in periphyton production. Less growth was found on water-logged branches of grapevine than on other kinds of water-logged wood.

Thomasson (1925) claimed that the same kind of periphyton grew on all non-living substrata. In the present study this was found to be true only to the extent that a characteristic mat was formed on all substrata, as small blue-green and green algae, diatoms, desmids, fungi, *Naidium*, Crustacea, Rotifera, and Protozoa were found there. However, this mat differed in appearance and composition because of absence, presence, or varying

amounts of different organisms. Thus, *Tolypothrix* grew abundantly on twigs and stones, sparsely on water-logged wood, and not at all on rope and glass slides. *Mougeotia* and other filamentous algae grew in large amount on twigs, but in smaller quantities on other substrata nearby. Twigs had more non-chironomid Diptera, but bore fewer hydras, even when bare, than other substrata. Periphyton on stone or wood was crusty, but not so on glass or rope. When on water-logged wood, it resembled that on stones by being hard and dense, but differed by being sparse, distributed in patches on the wood, and being no thicker than 1–2 mm. *Chaetophora* and *Tolypothrix*, heavily encrusted with marl, occurred in a green layer next to the wood, and were overlaid by a whitish layer of marl. This, in turn, was topped by a brown layer of diatoms, fungi, and sand grains.

Conversely, periphyton affected the substratum. It grew over the stones as a crusty, marly layer into which sand sifted until they were wholly or partly submerged under the soft, spongy material. It also increased the surface area of bulrushes. Waves, acting against this increased surface, could more easily push them over than when they were bare.

PERIPHYTON AND HEIGHT ABOVE BOTTOM

Whether a stone or a piece of wood lay on the bottom or was suspended some distance above it in the water made a difference in the appearance and composition of periphyton growing on it. When water-logged wood was hung higher than 20–30 cm above the bottom, its dense periphyton became soft and filmy by the abundance of filamentous algae like that on twigs at the same level. Twigs of brush shelters lying on or next to the bottom had a different growth from that on twigs above them. Wooden stakes were covered with a luxuriant growth down to 20–30 cm above the sand. When bulrush culms lay on the sand their growth was similar to that of water-logged wood. To determine the relation between periphyton and height above the bottom, dry aspen twigs and pieces of dry driftwood were nailed to stakes standing in water one meter deep. They were spaced 5 cm apart and parallel to the bottom. After four weeks' exposure the lowest stick had a few scattered colonies of *Rivularia* on it and isolated patches of thin fungus mat. Diatoms and green algae were scarce with but few *Pleuroxus*, *Chironomus*, and *Euchlanis*. Topmost sticks had much more fungus-diatom mat and an appreciable quantity of filamentous green algae. They had some *Stylaria*, *Ilyocryptus*, and different species of *Chironomus* in addition to those animals found on the lowest sticks. On intervening pieces occurred all gradations between sparse growth at the bottom and greater amount at the top. The higher above bottom, the more abundant was the fungus-diatom mat. The influence of substratum was seen in the fact that aspen twigs had more periphyton than driftwood.

Biotic Relationships of Periphyton

fish and periphyton

According to observations made by Smith as quoted by Reighard (1915), suckers used periphyton as food in Douglas Lake. The writer also has seen small fish put their mouths against bulrushes, move their jaws, and disturb the periphyton. When examined, periphyton was found to have been removed from the place touched by the fish.

changes within periphyton

Within periphyton itself many changes took place. Miller (1936) observed the decrease of hydras in late summer and suggested that, on bulrushes, they were displaced by the fungus-diatom mat. The present study shows that, as the mat increased in area and thickness, the number of hydras became smaller and smaller. Live culms had two to three times as many hydras as dead ones. They were found later in the season on live culms since the mat was not built up as quickly as on dead ones. When hydras were abundant on dead culms, the mat was usually sparse or localized in patches.

This felted mass of fungi and diatoms may have brought about changes in colonies of *Gloeotrichia* by reducing light and pressing upon them. When young, the colonies were soft and clear, but toward the end of summer, large numbers of them were brown, hard, and crusty with contained marl. They were flatter than young colonies.

In general, oligochaetes were numerous where the mat was thick, such as on dead culms, upon which were two to three times as many as on live culms (Tables 3–8). On live culms there was marked increase in the number of annelids as the summer wore on until, as the mat increased, there were as many worms as on dead culms.

Periphyton on stones was composed of three layers that differed in amount of marl deposited and the organisms present. Sand, diatoms, and masses of *Scytonema* colored the outermost layer brown and were felted together by the usual tangle of fungous fibers reinforced by *Bulbochaete* and *Chaetophora* filaments and branches of bryozoan colonies. The whitish second layer was composed of diatom-fungus mat and *Tolypothrix* trichomes surrounded by marl. Dissolving away marl with acid revealed fungus fibers and small, round, blue-green algae as the main components. The same materials found in the second layer made up the layer next to the stone. Here trichomes of *Tolypothrix* were white instead of green and were embedded in a hard, white, dense mass of marl that was hard to cut loose from the stone.

Changes in periphyton on stones appear to have been brought about largely by formation of marl and binding of sand. Trichomes of *Tolypothrix* first served to bind the mat together, including sand caught in the mat,

then marl cemented all components into one solid mass. This hardened layer then served as a substratum from which *Tolypothrix* could build.

When a *Tolypothrix* trichome from the middle layer was examined closely, a matted sheath was found surrounding all but its tip. Marl was found only in the sheath, but not on the trichome. The action of *Tolypothrix* may have caused deposition of marl which, once formed, was held by the mat. In this deposit were found the small blue-green algae already mentioned, as well as diatoms, both living and dead. Marl could have been deposited by the diatoms as well as the algae, but they could have become entangled and imprisoned without having taken part in its formation.

The Populating of Clean Surfaces

Experiments were conducted to learn the order in which periphyton organisms populated clean substrata. In carrying this out with bulrushes, only those of similar height, thickness, and power to remain erect were selected. They were wiped clean with a soft cloth as they stood in the water, marked, and left standing. Within three days these culms had a sparse population of diatoms, a few small green and blue-green algae, and fungus threads. Hydras and *Sida* were abundant when plentiful on other bulrushes. Eggs of snails and, occasionally, of chironomids were seen. Wherever these had been attached, fungi and diatoms were more abundant than usual.

At the end of a week, diatoms, fungi, and various algae had increased to such an extent that chironomids could form tubes and a few naids could inhabit the tangle. After two weeks the familiar structure of periphyton was to be seen, so much so that it was difficult to see any difference between bulrushes with scant growth and those that had been cleaned two weeks before. Several bulrushes, cleaned in 1938, were found in 1939. They had periphyton as thick as any untreated bulrush that had stood through the winter; it was also of the same nature.

Gloeotrichia played a minor part in repopulating cleaned culms, there being only one-tenth or less on them in comparison with uncleaned ones. In some instances, chironomid larvae and naids occurred in larger numbers on cleaned culms than on those that had not been touched.

It was impracticable to clean stones taken from the water because marl was embedded in their surface, so stones, about 30 cm in diameter, were taken from the bank, washed, and dropped in water about one meter deep. After a week's exposure, eggs of snails and chironomids, a very few diatoms, and a few *Sida* occurred on them. A week later, they felt slippery and examination revealed bacteria, many diatoms, a few chironomids, and *Sida*. At the end of a month, the accumulated diatomaceous growth had been supplemented by *Tolypothrix* and fungi. Sand had settled into the tangle, which, with particles of marl, made it feel granular.

Some chironomid larvae occurred on these stones during the first few

days of submergence. They belonged to species commonly found on all substrata studied. They made tubes of transparent material which, with their areas of attachment, provided places to which diatoms and small algae could become fastened.

At the end of the first year, the growth was thin, light, and granular, composed mostly of diatoms and fungi bound together and to the stone principally by *Tolypothrix*. Near and at the surface of this growth occurred *Bulbochaete* with a scattering of desmids and various green and blue-green algae.

Most important feature in building periphyton on stones seemed to be deposition of marl which cemented all enclosed material to the stones. *Tolypothrix* acted as forerunner, as they attached to the stone, helped form marl, and thus provided a base upon which *Bulbochaete* and *Chaetophora* could build. As the underlying layer became denser with marl, *Tolypothrix* appeared to grow out. The brown, diatomaceous layer was always on top of *Tolypothrix* and the marl. After another few years, the characteristic three-layered condition already described could be expected to occur.

The order of growth on twigs of brush shelters, immersed in water for the first time, was followed over a period of four years. Diatoms and fungi were the first organisms to be seen on the twigs. A very few were found after one week's exposure. At that time the wood felt slippery. After two weeks, tufts of fungi had started growing next to cracks in the bark. A week later, a light down appeared composed of fungi, diatoms, a few filamentous, grass-green algae, and an occasional filament of blue-green algae, such as *Lyngbya* or *Oscillatoria*. A short time later, a few solitary colonies of *Tolypothrix* appeared in the mat.

At the end of a year's submergence, periphyton showed great development, and there was appreciable increase on almost all brush shelters in centrifuged volume and dry weight. The only organisms showing no increase during the second year were Rivulariaceae and *Pelmatohydra*. On these same brush shelters, no appreciable increase was observed during the third and fourth years, of the total amount of periphyton. After so long a submergence some evidence of stratification was seen in the periphyton on twigs. As on stones, the cause of it was formation of marl, which was most abundant around *Tolypothrix* filaments next to the wood.

The Limnological Role of Periphyton

Periphyton is one of the productive assemblages of organisms within a lake, since many plants within it are capable of manufacturing food. In that respect it occupies a position similar to that of plankton and benthos. All three groups have saprophytic plants, herbivores, and carnivores which gain nourishment from food produced by green plants. All three give organic and particulate matter to the water. These materials are exchanged through the medium of water.

Dissolved organic material is used by certain periphyton organisms, such as bacteria, Algae, fungi, diatoms, some Protozoa, and possibly sponges (Welch, 1935). Particulate matter is used as food by Protozoa and such water strainers as Bryozoa and Rotifera. Organic material, both dissolved and particulate, may come originally from plankton organisms or from periphyton. Furthermore, organic material given off by periphyton may pass to plankton or benthos. It also contributes to the nourishment of higher aquatic animals whenever it is eaten by fish. Within itself, herbivores such as Chironomidae, *Naidium*, and Entomostraca eat loose particulate material, and the carnivorous *Pelmatohydra*, Turbellaria, and *Chaetogaster* prey upon animal forms. Thus periphyton is itself a food complex and is an integral part of the food complex within a lake.

Since periphyton contains marl-building plants, both calcium and carbon dioxide are lost through their activities. In this way, periphyton affects chemical conditions in a lake. If the resulting marl is buried, the loss is permanent.

Periphyton affects many submersed objects in some way or another, or at one time or another. One effect may be produced by penetration of substratum by its organisms, weakening the bulrush or twig so that it breaks and sinks to the bottom. Periphyton also increases surface area exposed by a bulrush or twig to wave action so that it would be more easily broken off. It also aids in burial of stones by forming a marl crust over them. Thus it builds up the bottom and makes it smoother. In this way periphyton itself may eventually become bottom deposit.

The surface available to periphyton is reduced when stones become covered by sand and dead bulrushes fall to the bottom. Thus periphyton tends to destroy its own habitat. The lost surface upon which it would have grown is replaced each year by bulrushes and other plants growing anew each spring. Additional surface becomes available whenever branches of trees become submerged. If plants and wood are suspended in water, more periphyton can grow on them than if they lie on the bottom.

Periphyton is also a suitable habitat for certain kinds of organisms. Chironomid larvae build tubes within the fungus-diatom mat, and oligochaetes and crustaceans find shelter and hiding places within it. In the rigorous habitat of Big Shoal (as described by Moffett, 1943) periphyton has more organisms per unit area than benthos. However, since bulrushes occupy only a small area, total productivity of benthos exceeds that of periphyton.

Periphyton is a unique group of organisms in a lake. It is apart from benthos and plankton and yet similar to them both. Like benthos, it occupies a place where water comes in contact with a surface. The substratum furnished by the stone or plant upon which it grows is merely an extension of the bottom. Though it resembles benthos, yet it has a position up in water, somewhat like that of plankton.

Periphyton occupies a position where components of both plankton and benthos come together. Plantonic organisms, such as diatoms, desmids, and small Algae, are caught and held in the tangle of attached forms. Fungi, Rivulariaceae, Hormogonales, and sheathed or stalked diatoms are similar to benthic forms in that they adhere to a solid support. Notwithstanding resemblances of periphyton to benthos and plankton, it has developed a distinctive character of its own.

Summary

1. One hundred fifteen species of organisms, distributed among 98 genera, were found in periphyton. Only 13 genera were represented by more than one species.

2. Numerically dominant forms found on all substrata were: Fungi, Rivulariaceae, Chlorophyceae, Bacillareae, Naididae, Cladocera, and Rotifera.

3. Wave action caused periphyton on bulrushes to be sparse near the surface of the water and most abundant in the stratum 40–80 cm below the surface.

4. Severe wave action was followed by marked reduction in periphyton. Fluctuations in the number of organisms corresponded roughly to the amount of weather disturbance.

5. Periphyton was reduced in amount near shore where waves caused surf. Likewise, bulrushes in sheltered situations had more periphyton than those in situations exposed to more wave action at the same depth.

6. When washed off bulrushes, periphyton became a part of the plankton.

7. Different kinds of living substrata had the same species growing upon them, but differed with respect to the numbers of individuals present, so that periphyton on each substratum had a characteristic appearance.

8. The abundance and type of periphyton were influenced by the kind of dead wood upon which it grew. Each non-living substratum was found to have a characteristic periphyton growing on it modified by whether the substratum lay on the bottom or was suspended some distance above it.

9. When a living or nonliving substratum was cleaned and then immersed in water, it became covered with the periphyton characteristic of that substratum.

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